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Stimulation of plants by carbon disulphide

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The problem of stimulation of plants by minute doses of chemicals, which are poisonous in higher concentrations, has long been an interesting one. Raulin (1) in 1869 was probably the first to undertake work of this kind, using a nutrient solution made up of a large number of substances as a culture medium. As the stimulant, Raulin added to his nutrient solution small amounts of metallic salts, such as silver nitrate, platinum dichloride, or copper sulphate, and found that cultures of *Aspergillus niger*, grown in these solutions produced a more luxuriant mycelium than cultures to which nothing had been added. Pfeffer (2) in 1895, by means of comprehensive experiments, determined that such a complicated nutrient solution was unnecessary and originated a number of solutions which have been and are still extensively used in work of this kind. Benecke (3), in the same year, published a paper in which he also gave a much simpler normal solution than Raulin's but slightly different from Pfeffer's.

Richards (4), using the latter's solution with the addition of traces of zinc, iron, sodium, lithium, and other salts, obtained a heavier growth of *Aspergillus niger* and *Penicillium glaucum* than in cultures to which none of the above were added, demonstrating that Raulin's solutions really resulted in stimulation. Ono in 1900 corroborated Richards's results and also worked out the effect of these salts on certain algae. He found that algae as a rule have their point of greatest stimulation at a much lower concentration of the salt but in other respects are similar to fungi. Richards (5) and Ono (6) determined that the economic coefficient of sugar is considerably lower in the cultures to which salts had been added than in the controls, proving that stimulated fungi require a smaller amount of carbohydrate food in proportion to the quantity of waste acid produced.

Since this time many other investigators have worked on this problem, obtaining similar results. Kahlenberg and True (7) formulated a law which they gave as an explanation of this stimulation phenomenon. They claim that since the chemical and physical properties of solutions are due to the properties of the ions dissociated in the solution and of the undissociated molecules, then the physiological properties of a solution are due to the same factors. The authors worked out this theory with lupine seeds, the germination of which was accelerated by dilute solutions of electrolytic salts. They claimed that this stimulation was due to the hydrogen and metallic ions in the solutions. Heald (8) working with seeds of other plants obtained similar results and also attributed them to the electrolytic dissociation. Stevens (9) working with fungus spores applies this same theory. Iwanoff (10) claims that metallic salts are poisonous to plants in proportion to the atomic weight of the metal, the heavier metals being more poisonous than those of smaller atomic weight. In his opinion, the same is true of the alcohols, the lower alcohols (methyl and ethyl) being less poisonous than those of higher molecular content, such as propyl and butyl. Steinberg (11), in a recent paper on the stimulation of *Aspergillus*, attributes the stimulation to the increase in H ion content when zinc salts are added to the nutrient solution. It is not obvious, however, that the action of such oligodynamic substances is due to the hydrogen ion concentration alone, especially since we find non-electrolytes, such as ether, chloroform, and other anaesthetics, exerting a stimulatory influence. Carbon disulphide, being a very volatile liquid, which is non-dissociable in aqueous solution, also comes in this category.

Various authors have worked with ether and chloroform, although few have done anything with carbon disulphide. Townsend (12) in his experiments with *Avena* seeds found that if dormant seeds were exposed to a moist concentrated atmosphere of ether for a short time, or to a weaker atmosphere of ether for a longer period, the seeds germinated sooner and grew more rapidly than under normal conditions. This acceleration lasts for some time and gradually disappears. In a later paper (13) Townsend verified his results with other seeds: *Zea Mays*, *Cucurbita*, *Phaseolus*, etc. He also found that dry seeds, exposed to an atmosphere of HCN gas (14), germinated more rapidly than those not exposed although this advantage did not last for any appreciable time. Miss Latham (15), working with *Sterigmatocystis nigra*, determined that cultures of the fungus grown on nutrient media and exposed to chloroform vapor, produced a more luxuriant growth with a greater dry weight than similar cultures unexposed. Furthermore the oxalic acid formation was lower per unit dry weight in the stimulated cultures.

Johannsen (16) was the first to discover that exposing dormant buds to an atmosphere impregnated with ether forced the buds to open earlier than normal. Chloroform has the same effect but is more powerful, less being needed to bring about the same result.

No attempt has been made to cover the whole field of the very voluminous literature on this subject. A comprehensive account may be found in Czapek's "Biochemie der Pflanzen," second edition, Vol. 1, page 147 *et seq.*, 1913.

Among the investigators who experimented with carbon disulphide, none used it in gaseous form but either in pure liquid state or in aqueous solution. Sirker (17) in Japan found that mulberry bushes, grown in soil previously treated with CS_2, produced more branches, higher plants and more leaves with a greater dry weight for each individual leaf than bushes grown in untreated soil. Koch (18) in 1912 found the same thing with other plants. Koch asserts that the carbon disulphide is not used as a carbon source, nor does it act as an insecticide in killing off the harmful lower organisms in the soil, since under such circumstances a larger amount of the CS_2 would be more beneficial. This, however, is not the case, a larger amount of the CS_2 being harmful, and the stimulation takes place only when the compound is added in minute quantities. Fred (19) in the same year stated that carbon disulphide added to the soil in dilute solutions stimulated the growth of soil bacteria, the nitrogen-fixing forms in particular, so that the quantity of nitrogen built up into higher compounds was measurably increased over normal. In a later paper Fred (21) corroborated his earlier results and concluded that while after treatment with carbon disulphide the soil showed a reduction in the number of microorganisms, it was followed by a great increase and an increase also in the by-products of their action. With relatively strong applications of carbondisulphide to the soil, corn and oats seemed deleteriously affected, while mustard and buckwheat were benefitted, as shown by increase in dry weight. In acid soil, clover is also stimulated.

The experiments described below, which further test the effect of carbon disulphide on plants, were performed in the

Botanical Laboratories of Barnard College, under the supervision of Professor H. M. Richards, for whose advice and assistance the writer is greatly indebted.

In this work, while no attempt was made to cover every type or condition of plant tissues, a number of widely differing kinds of material were employed. The experiments fall into three groups, each of which could profitably be elaborated beyond what was attempted here. These three categories are as given below and will be considered as separate topics in the following discussion.

1. Stimulation of seeds and seedlings.
2. Stimulation of buds.
3. Stimulation of certain fungi.

Carbon disulphide is a clear, practically colorless liquid when pure, very inflammable and volatile. It has a disagreeable odor, especially when impure, because of the decomposition into other sulphur compounds, hydrogen sulphide in particular (see Graham, 20). It is soluble in all proportions in alcohol, ether, and chloroform, but only slightly soluble in water. The solubility in water, according to Graham, varies inversely as the temperature, as follows:

At 12°–13° C. 2.0 gms. CS_2 dissolve in 1 liter of water.
" 15°–16° " 1.91 " " " " 1 " " "
" 25°–27° " 1.68 " " " " 1 " " "
" 30°–33° " 1.45 " " " " 1 " " "

From these data, it was estimated by interpolation that at 20°–22° C. (average room temperature) about 1.8 gms. CS_2 dissolves in 1 liter of water.

In the following paper, the concentrations of the solutions used were determined in terms of molecular solutions. The molecular weight of carbon disulphide is 76.125, and if 1.8 grams dissolve in 1 liter of water at approximately room temperature, then a saturated aqueous solution is 0.0235 of a molecular solution. More dilute solutions were prepared from this, in fractions varying by 1/2000M. No attempt was made to determine or maintain the exact concentration closer than this, because carbon disulphide is so easily vaporized and a certain amount of that in solution is continually volatilizing out. In cases where the experiments lasted over a few days, the solutions were renewed at intervals of two or three days.

1. STIMULATION OF SEEDS AND SEEDLINGS

The first phase taken up was to determine if there was any stimulation of young seedlings by dilute solutions of carbon disulphide. Townsend (**12**, **13**, **14**) tested the effect of ether vapor and hydrogen cyanide gas on different kinds of seeds, by soaking seeds in water for twenty-four hours and then putting in an airtight damp chamber containing ether vapor. The exposed seeds germinated more quickly than unexposed controls, but whether left in ether chamber or removed immediately after germination, the stimulated seedlings soon lost their advantage, and five days after germination the control seeds equaled the stimulated in growth. Likewise dry seeds exposed to HCN gas for a short time and then soaked in water germinated more rapidly than seeds not treated with the hydrogen cyanide. However in every case, growth was equal after a week.

In the following experiments, wheat grains (*Triticum sativum*) were used. One hundred grains were soaked in the CS_2 solution for twenty-four hours. Seed pans were filled with moist sphagnum, covered with damp cheese cloth, and grains planted out on top of this. They were then covered with a second layer of cheese cloth, with a pad of moist sphagnum on top of the whole. Pans were kept under a shelf in the greenhouse for three or four days, taking care not to allow the sphagnum to dry out. The seedlings were then uncovered, epicotyls measured and the average taken of those germinated. It was found that the saturated solution completely inhibited growth, while the seedlings in the other solutions grew as shown in TABLE I.

TABLE I

AVERAGE GROWTH IN MILLIMETERS OF EPICOTYLS OF WHEAT SEEDLINGS AFTER BEING SOAKED IN FOLLOWING CS_2 SOLUTIONS FOR 24 HOURS AND LEFT TO GERMINATE FOR 3 OR 4 DAYS

SERIES 1. Germinated 4 days

Exp.	A.	B.	C.	Average	Avg. per day
M/2,000			37.7	37.7	9.4
M/4,000	39.7	35.2	38.5	37.8	9.4
M/6,000	40.6	29.2		34.9	8.7
M/8,000	34.8	31.1	41.3	39.1	9.8
M/12,000	38.3	34.1		36.2	9.1
M/16,000	42.7	33.2	37.6	37.8	9.5
M/22,000	41.2	28.9	43.4	37.8	9.5
M/32,000	40.0	36.6	39.4	38.7	9.7
M/40,000			41.5	41.5	10.4
Control	35.8	33.0	36.6	35.1	8.8

TABLE I (*con.*)

SERIES II. Germinated 3 days

Exp.	D.	E.	Average	Avg. per day
M/2,000	13.6	10.0	11.8	3.9
M/4,000	13.3	13.8	13.6	4.5
M/8,000	16.8	14.5	15.7	5.2
M/16,000	14.7	13.7	14.2	4.7
M/22,000	14.9	14.2	14.6	4.9
M/32,000	18.7	14.4	16.6	5.5
M/40,000	12.7	15.3	14.0	4.7
Control	11.1	13.6	13.3	4.4

Although these results show some irregularities due to the comparatively small number of cases, they also reveal a marked stimulation of growth especially in the solutions between M/22,000 and M/40,000 in CS_2 content. The stimulation in the three day experiments is proportionally greater than in the four day instances, showing that the stimulation tends to diminish, and growth tends to approach the normal after an interval, just as Townsend found.

An experiment with *Vicia Faba* seedlings was carried out in the following manner. The seeds were planted and allowed to germinate until the hypocotyls reached a convenient length to measure. A number 400 cc. bottles were almost filled with Knop's nutrient solution and enough CS_2 solution was added to make of desired concentration. The bottles were then fitted with corks, each cork having three holes bored in it, which were just small enough to prevent the seeds from falling through. The seedlings grown as above, were then washed in distilled water, hypocotylsm easured, and arranged in culture bottles so that seed rested on top of cork and hypocotyl extended through the hole into the solution. The bottles were placed in a dark chamber in the green house (temperature varying from 18° to 25° C.), the hypocotyls were measured every twenty-four hours and the daily growth computed.

TABLE II

AVERAGE GROWTH IN MILLIMETERS OF THREE HYPOCOTYLS OF *Vicia Faba* SEEDLINGS, PLACED IN NUTRIENT SOLUTIONS CONTAINING CS_2 TO MAKE OF FOLLOWING CONCENTRATION, EACH EXPERIMENT COMPRISING TWELVE SEEDLINGS

	M/2,000	M/4,000	M/6,000	M/8,000	M/20,000	M/40,000	Control
Exp. A.							
1st day	5.3	6.5	13.0		13.7		7.0
2nd "	2.2	5.4	11.7		16.1		9.5
Total	7.5	11.9	24.7		29.8		16.5
Avg.	3.8	6.0	12.4		14.9		8.3
Exp. B.							
1st day		18.2	18.2	22.7	22.9	17.8	18.9
2nd "		19.4	23.4	21.6	21.0	16.2	19.6
3rd "		21.4	19.0	19.7	15.8	8.1	14.4
4th "		19.2	19.2	23.5	17.0	17.7	16.3
Total		78.2	79.8	87.5	76.7	59.8	69.2
Avg.		19.6	20.0	21.9	19.2	15.0	17.3
Exp. C.							
1st day	16.6	14.6	13.6	13.7	14.7	16.6	19.3
2nd "	10.5	16.0	18.7	21.8	21.6	16.0	17.5
3rd "	14.1	18.4	18.0	29.0	26.7	15.5	19.7
Total	41.2	49.0	50.3	64.5	63.0	48.1	56.5
Avg.	13.7	16.3	16.8	21.5	21.0	16.0	18.8
Exp. D.							
1st day	9.5	16.8	10.8	20.0	39.0	1.5	19.8
2nd "	7.0	11.5	11.0	18.0	12.5	11.0	16.5
3rd "	8.0	14.0	12.9	24.5	18.5	13.2	17.0
Total	24.5	42.3	34.7	62.5	70.0	25.7	53.3
Avg.	8.2	14.1	11.6	20.8	23.3	8.6	17.8
Total average of the four experiments (i.e. twelve examples).							
	8.6	14.0	15.2	21.4	19.6	13.2	15.6

TABLE II shows a distinct stimulation in the growth of hypocotyls of *Vicia* seedlings, in the M/6,000 to M/20,000 CS_2 solutions, the average greatest stimulation being in the M/8,000 dilution, although the M/20,000 shows a greater acceleration in some instances. In the M/40,000 concentration, the CS_2 content has become so dilute that it no longer has any effect on growth. In the higher concentrations, the M/6,000 solution caused a marked stimulation in Exp. A and B, although in other cases growth is not as great as normal in these dilutions. Although the M/4,000 and M/2,000 solutions do not entirely inhibit growth, they do retard it below normal. Complete inhibition was found in the saturated CS_2 solution, but no dilutions were tried between that and the above.

Koch (18) tried similar experiments with *Helianthus annuus* and *Cucurbita Pepo* seeds, letting the seeds germinate and then placing them in the dark, with their hypocotyls in solutions containing 0.1 and 0.05 cc. CS_2 to 1000 cc. water for thirteen to fourteen hours. In one case only, in the solution containing 0.05 cc. CS2 to the liter(about M/150 solution), did he obtain growth higher than normal. This being only a single instance was probably an accident due to the solution being weaker than intended and cannot in any sense be called a stimulation. Koch did not try any solutions weaker than this and therefore did not reach the stimulatory region but really only determined that carbon disulphide acted as an inhibitory agent.

2. STIMULATION OF DORMANT TWIGS

Johannsen (16), investigating the effect of ether on dormant twigs, found that they were stimulated so that the buds opened sooner and developed more rapidly when exposed to ether vapor for twenty-four to forty-eight hours, than when unexposed. When using chloroform a much smaller amount was necessary to produce the same result (9 grams of chloroform giving the same acceleration as 40 grams of ether).

With these results in view, experiments were carried out to see if vaporized carbon disulphide would stimulate buds to open. Willow twigs were cut from trees outdoors which had been subjected to winter conditions and were probably frozen in spite of the general mildness of the winter. The lower three or four inches of the stem were placed in a bottle of water and a large bell-jar put over them. Pieces of filter paper, moistened with 10 cc. of carbon disulphide were quickly inserted under the bell-jar. The whole was placed in a pan of water making a water seal so that the carbon disulphide, which vaporizes almost immediately, could not escape from the bell-jar. The twigs were left in this atmosphere (approximately saturated with CS_2 gas) for periods ranging from ten minutes to eighteen hours. They were then removed, the stems were put into fresh water and with a control placed in the greenhouse.

The results of a number of experiments can be summarized as follows. After three days, the twigs exposed ten and twenty minutes began to develop, the buds showing patches of green at the tips. After seven days, the buds on the twigs exposed thirty minutes were open considerably. One of the hour experiments showed slight greening of the upper buds but other specimens gave no evidence of development. After nine days, the control (not exposed to CS_2 at all) had two buds developing. Twigs exposed ten, twenty and thirty minutes continued to show better bud development for two to three weeks longer, after which the condition of all tended to become the same. Twigs exposed for one and a half hours or for two hours started to open but after a day or so became brown and withered, while those exposed for four hours or more showed no signs of development at any time, indicating that the protoplasm itself must have been killed.

3. STIMULATION OF CERTAIN FUNGI

As stated above, there has been a vast amount of work done on stimulation of fungi by metallic salts and other chemicals. Because of this, a number of experiments were set up to test the effect of carbon disulphide on fungi.

To determine the effect of dilute solutions of carbon disulphide on the germination of spores of *Rhizopus nigricans* and *Sterigmatocystis nigra*, hanging drop slides were used. Small glass rings were attached to microscope slides by means of a solution of dextrin in water (vaseline is not practicable since carbon disulphide is very soluble in it). The medium used for the germination of the spores was prepared according to the following formula (see Richards, 4):

Potassium phosphate	0.5 gm.
Magnesium sulphate	0.25 gm.
Ammonium nitrate	1.0 gm.
Ferrous sulphate	trace
Sugar	5.0 gms.
Distilled water	100 cc.

To this was added 5 gms. of gelatine, and the mixture was then heated in water bath. When the gelatine was completely solved, the medium was filtered tubed (10 cc. to the tube) and sterilized. Before the gelatine hardened, the CS_2 solution was added to make of desired concentration.

A small drop of this gelatine was put on a clean cover glass and inoculated with fungus spores. After inverting the cover glass, and sealing on to the glass ring the slides were left standing at room temperature under a bell-jar containing moist filter paper to prevent slides from drying up. After some hours, slides were examined microscopically for germination, and where possible the germination-tubes were measured by means of a standardized micrometer eye-piece.

According to TABLE III. solutions of carbon disulphide in nutrient gelatine varying from M/16,000 to M/40,000 in concentration, stimulate spores of *Rhizopus nigricans* and *Sterigmatocystis nigra* to germinate sooner than in the same media but without the CS_2. The point of greatest stimulation lies between the M/32,000 and the M/40,000 solutions.

In another type of experiment with *Sterigmatocystis* spores, the stimulation of growth was measured by the increase in dry

TABLE III

AVERAGE GROWTH IN MICRONS OF 10 GERMINATION TUBES OF FUNGOUS SPORES, INOCULATED ON NUTRIENT MEDIA TO WHICH CS_2 HAD BEEN ADDED

RHIZOPUS NIGRICANS

No. of hours	M/800	M/8,000	M/16,000	M/22,000	M/32,000	M/40,000	Control
Exp. A.							
24	10.6	11.9	59.9	over 300	over 300	over 300	250.
Exp. B.							
13½	no	no	no	no	6.7	52.6	no
15	no	no	no	13.9	16.4	83.2	no
18	5.0	no	no	70.0	50.4	over 300	45.9
20½	26.9	no	9.5	103.9	76.7	over 300	59.5
Exp. C.							
13	29.7	57.4	over 300	139.2	over 300	over 300	no
14	59.6	over 300	over 300	over 300	over 300	over 300	no
17	over 300	" "	" "	" "	" "	" "	98.6
Exp. D.							
13	129.6	203.6	——	13.2	8.1	10.1	no
15	281.1	313.0	——	22.7	24.1	46.5	14.8
18	over 300	over 300	——	44.3	73.6	79.3	44.5
Exp. E.							
14	67.5	68.3	——	20.4	39.2	21.0	10.9
17	101.6	148.1	——	62.2	84.3	43.4	25.5
19	127.4	over 300	——	91.6	96.9	88.2	52.6

TABLE III (*con.*)

STERIGMATOCYSTIS NIGRA

No. of hours	M/800	M/8,000	M/16,000	M/22,000	M/32,000	M/40,000	Control
Exp. A.							
29½	44.5	over 300	50.7	——	56.5	20.4	no
48	126.2	" "	over 300	——	over 300	over 300	224.9
Exp. B.							
15	no	no	no	no	no	6.4	no
20	no	no	no	no	no	75.6	no
35	no	no	no	no	no	over 300	no
65	no	—	over 300	over 300	over 300	" "	start
Exp. C.							
19	no	no	no	no	117.0	124.9	no
25	no	no	no	137.5	over 300	over 300	no
27	no	no	no	over 300	" "	" "	no
68	no	no	no	" "	" "	" "	no
91	no	no	over 300	" "	" "	" "	start
Exp. D.							
19	no	no	78.4	57.1	over 300	152.3	no
25	no	no	over 300	over 300	" "	over 300	no
74	no	no	" "	" "	" "	" "	start

weight of the germinating hyphae. In their experiments 150cc. Erlenmeyer flasks were used as culture bottles and, with pipettes and other apparatus, were cleansed with cleaning solution, rinsed in tap water a number of times, then in distilled water and finally in double distilled water. The same solution as in the former experiment, but without the gelatine and with double distilled water was employed as a culture medium. The trace of ferrous sulphate was introduced by adding one drop of a saturated solution of ferrous sulphate in double distilled water.

After the nutrient solution was made up, it was inoculated in bulk with the *Sterigmatocystis* spores, and 50 cc. of the inoculated solution pipetted into each flask. The aqueous CS_2 solution (also prepared with double distilled water) was added last. The flasks were then corked by means of a mercury air trap, which would allow air to come into the flask, but would not allow any gas to escape from the flask and thus change the CS_2 ratio.

After being stoppered, the flasks were left in a dark chamber at room temperature and, as a preventive measure, the controls were put in a different compartment from those to which carbon disulphide had been added. After five days, the flasks were removed, pads filtered off on weighed filter paper and dried in hot air oven at 70° to dry weight. No attempt was made to determine the CO_2 or acid production, although this would have been an interesting point to investigate.

Although growth was not wholly normal in the controls, presumably due to lack of adequate circulation which may have caused carbon dioxide to accumulate, nevertheless the gross appearance of the stimulated was strikingly different from that of control specimens. The solutions containing CS_2 in the most optimum concentrations bore tough pads, thicker and considerably heavier than normal. All the stimulated pads were wrinkled and curled, and slightly yellow on the under surface. Practically no spores were produced, although in some cases a few yellow sporangia were observed. The control felts on the other hand were thin and tender in texture, and more or less covered with black spores. However, if further experiments were to be carried out, a more perfect system of maintaining the concentration of CS_2 in the flasks would have to be devised in order to obtain absolutely normal controls.

TABLE IV

DRY WEIGHT IN MILLIGRAMS OF CULTURES OF STERIGMATOCYSTIS NIGRA, GROWN IN NUTRIENT SOLUTION TO WHICH CS_2 HAD BEEN ADDED

Exp.	Control. No CS_2	M/80,000	M/40,000	M/20,000	M/10,000	M/5,000
A	439	838	800	740	585	270
B	442	1028	815	748	675	370
C	530	765	1035	495	490	—
D	578	788	740	810	540	—
Avg.	497	855	848	698	573	320

The results of TABLE IV are sufficient to indicate that there is a marked stimulation in cultures to which carbon disulphide has been added. The region of greatest stimulation is in the flasks M/80,000 and M/40,000 CS_2 solutions, the more dilute concentration being slightly more advantageous than the other.

Complete inhibition was not found in any of the experiments tried, although the flasks containing M/5,000 solution only produced felts of approximately three-fourths of the normal weight. In some instances the M/10,000 acted slightly as an inhibitor so that growth below normal was produced.

SUMMARY

All things considered, the results of this investigation lead one to conclude that carbon disulphide acts on plants as many other chemical stimulants do. When applied either in aqueous solution or in vaporized condition it inhibits growth, if given in too concentrated a solution or if vapor is used for too long a time.

When used in dilute amounts, carbon disulphide has the ability to stimulate:

(1) Dormant protoplasm, as in the case where twigs exposed to CS_2 vapor for a short period of time quickly resumed their growth;

(2) Active protoplasm, as in case where the hypocotyls of *Vicia* seedlings elongated more rapidly upon the addition of small amounts of CS_2;

(3) Conidial spores of certain fungi which germinated sooner and produced germination tubes elongating more rapidly, the stimulation causing also causes an increase in dry weight.

Carbon disulphide acts also as other stimulants do, in that the acceleration of growth lasts only for a certain period of time, and then growth tends to reach normal again. This fact was shown in the twig experiments and those with *Triticum* grains. The same would probably be true of the other experiments if left running for a sufficient length of time.

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